APPENDIX. Continued.

Species and authority	Herbarium	Collector and number	Country
J. martiusii (Pohl) Baillon	FLAS, DAV	Dehgan & Webster BD86.346	Brazil
J. mcvaughii Dehgan & Webster	DAV	Dehgan B74.206	Mexico
J. mollissima (Pohl) Baillon	FLAS	Dehgan & Webster BD86.318	Brazil
J. moranii Dehgan & Webster	DAV*	Howell 10606	Mexico
J. multifida L.	MO, KEW	Valeur 684	Dominican Republic
J. mutabilis (Pohl) Baillon	FLAS	Dehgan & Webster 312	Brazil
J. neopauciflora Pax	TEX, NY, GH, DAV	Webster et al. 17319	Mexico
J. nudicaulis Benth.	MO	Dodson & Dodson 12941	Colombia
J. olivacea Muell. Arg.	US	Pringle 6348	Mexico
J. ortegae Standley	MIN*	Ortega 6455	Mexico
J. pachypoda Pax	M*	Fiebrig 3042	Bolivia
J. pauciflora Griseb.	NY	Ekman 16169	Cuba
J. peiranoi Lourt. & O'Donn.	MO	O'Donell & Meyer 5308	Argentina
J. platyphylla Muell. Arg.	DAV	Webster & Lynch 17032	Mexico
J. podagrica Hook.	MICH	Breedlove 11810	Mexico
J. pohliana Muell. Arg.	M	Luetzelburg 26802	Brazil
J. pseudocurcas Muell. Arg.	DAV	Webster et al. 11746	Mexico
J. purpurea Rose	BM*	Palmer 785	Mexico
J. ribifolia (Pohl) Baillon	KEW*	Gardner 2303	Brazil
J. ricinifolia Pax	UC	Venturi 2350	Argentina
J. riojae Miranda	F**	Miranda 2111	Mexico
J. rufescens Brandegee	UC*	Purpus 4049	Mexico
J. rzedowskii J. Jiménez Ramírez	FLAS**	Jiménez s.n.	Mexico
J. standleyi Steyermark	MICH	Matuda 2260	Mexico
J. stevensii G. L. Webster	MO	Stevens 22902	Nicaragua
J. sympetala Blake & Standley	BM, ENCB, GH, MICH, TEX, UC, NY	McVaugh 15637	Mexico
J. thyrsantha Pax & Hoffm.	MICH	Troll 455	Bolivia
J. tlalcozotitlanensis J. Jiménez Ramírez	FLAS	Lozano 38	Mexico
J. tupifolia Griseb.	DAV, GH	Webster et al. 198	Cuba
J. vernicosa Brandegee	UC**, GH	Brandegee s.n.	Mexico
J. weddelliana Baillon	CEN	Allem 669	Brazil
J. yucatanensis Briq.	CAS	Thorn & Lathrop 40462	Mexico

* Type.
** Isotype.

A PRELIMINARY CLASSIFICATION OF *EUPHORBIA* SUBGENUS *EUPHORBIA*

Susan Carter[1]

Abstract

During preparation of the Euphorbieae for the *Flora of Tropical East Africa*, most of the 250 plus species in *Euphorbia* subg. *Euphorbia* were examined, resulting in a new approach to their classification. Comments are offered on the principal systems to date, all of which have been based on vegetative characters. In the newly proposed system, certain character changes linked with increasing succulence and a reduction in size are used to indicate development from trees, to shrubs, and then herbs, as an advancement in adaptation toward survival in arid conditions. Features of the inflorescence, capsules, and seeds are considered to be the most important in deciding relationships between groups, while vegetative features are used as indicators of development within the groups. A system of two sections based on seed characters is proposed, and the relationships between eight proposed subsections are discussed.

In preparing an account of *Euphorbia* subg. *Euphorbia* for the *Flora of Tropical East Africa* (Carter, 1988), a linear sequence in as natural a progression as possible had to be devised to accommodate the recognized species. Within the subgenus at least 250 species are known, the majority of which are native to Africa (excluding Madagascar), the rest extending westward to the Canary Islands and eastward to the Arabian Peninsula, India, and Malaysia. Examination of the approximately 90 species known in East Africa, and many more outside the geographical area of the *Flora*, has led to the outline of the system that classifies species more satisfactorily and more naturally than hitherto.

Subgenus *Euphorbia* in its strictest sense (formerly section *Diacanthium* of Boissier, which includes the type species of the genus, *E. antiquorum* L.), encompasses one of the most well-defined groups within the genus *Euphorbia*. Its species possess succulent stems and branches, with the base of each leaf surrounded by a horny pad (the *spine-shield*) bearing a pair of spiny outgrowths (*spines*), and stipules modified as *prickles*. The paired spines may become fused to produce a single spine; and the prickles may occasionally be as large as the spines, but are usually much smaller and sometimes apparently obsolete. The extent to which the prickles are obvious has affected almost all classifications. Above the spine-shield, morphologically in the leaf-axil, is the *flowering-eye*, from which the inflorescence develops, consisting of a solitary dichasial cyme, or of a group of cymes. Some Madagascan species develop apparently similar horny structures bearing one or more "spines," but these are actually modified stipules, each with an expanded horny base that flanks the leaf-scar but does not surround it. In related species these stipular structures are often developed into bristly fringes. All these species belong to the subgenus *Lacanthis* (Raf.) M. G. Gilbert (Gilbert, 1987) and are confined to Madagascar, with the exception of a few species from eastern tropical Africa.

Systems for classification to date have been artificial in their subdivisions, some extremely so, separation relying solely on vegetative characters, using habit, number of stem-angles, and number of spines and prickles borne on the spine-shield.

The first classification, by Boissier in 1862, involved less than 30 species that are recognized as such today, but included also several that are unrelated, such as the Madagascan *Euphorbia splendens* Hook. (*E. milii* Des Moul. var. *splendens* (Hook.) Ursch & Leandri), now included in subgenus *Lacanthis* (Raf.) M. G. Gilbert. Boissier defined two groups within his section *Diacanthium*: *Biaculeatae* for those species with each spine-shield bearing two spines that he considered to be stipular; and *Triaculeatae*, with three "spines" that were, in fact, two large prickles and a single (fused) spine. He further divided *Biaculeatae* into species with cylindrical as opposed to angled branches, and the latter into those with compressed (two-angled) branches versus those with three or

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more angled branches. Most species fell within this last group. He thought that *Euphorbia venenifica* Kotschy, a single-spined shrub with spirally arranged tubercles, should probably be excluded from the genus; and he mistook *E. ingens* Boiss., a large tree species, for one without spines.

1862. Classification by Boissier of Groups in Section *Diacanthium*

Diacanthium
  Biaculeatae 2 spines
    Branches cylindrical
    Branches sharply angled or ridged
      Branches compressed
      Branches 3- or many-angled
  Triaculeatae 1 (fused) spine, 2 prickles

Since Boissier's (1862) treatment, attempts to classify an increasing number of species have resulted in the vast majority falling within a group identified by two spines on each spine-shield, and three to many branch-angles, including trees, shrubs, and dwarf herbs, often with little further delimitation.

In 1904, Pax published a classification for over 80 species in section *Diacanthium*, based primarily on the number of spines and prickles present on each spine-shield. Species were assigned to groups that he named *Monacanthae*, *Diacanthae*, *Triacanthae*, *Tetracanthae*, and *Intermediae*, this last group defined by additional "upper stipular" spines on each side of the flowering-eye. By far the largest group, in which he included the unrelated species *E. splendens*, was the *Diacanthae*.

1904. Classification by Pax of Groups in Section *Diacanthium*

Monacanthae 1 (fused) spine
Diacanthae (Biaculeatae Boiss.) 2 spines
  Herbs with tuberous roots
  Shrubs or trees; branches not winged
    Leaves present
    Leaves absent; branches 3–many-angled
  Shrubs or trees; branches winged
    Leaves present
    Leaves absent; branches 2–8-winged

Triacanthae (Triaculeatae Boiss.) 1 (fused) spine, 2 prickles
Tetracanthae 2 spines, 2 prickles
Intermediae 2 spines, rudimentary prickles, upper stipular spines sometimes present

A third system, using number of branch-angles with no mention of spines, was erected in 1907 by Berger to accommodate about 50 species in cultivation at La Mortola, a large garden on the Italian Riviera owned by Sir Thomas Hanbury, where Berger was curator. His groups, without formal ranking, bore only a vague resemblance to those proposed by Pax. They included *Splendentes* (the unrelated Madagascan species with terete leafy branches allied to *E. splendens*), *Grandifoliae* (terete branches and large leaves), *Scolopendriae* (short thick stem), *Compressae* (2–3-winged branches), *Trigonae* (3–4-winged branches), and *Polygonae* (4–13-winged branches). The greatest number of species were in this last group. Single-spined species were not included, as none were in cultivation at La Mortola.

1907. Classification by Berger of Groups in section *Diacanthium*

Splendentes Branches terete; leaves present, small
Grandifoliae Branches terete; leaves present, large
Scolopendriae Herbs with short thick stem; branches ribbed; leaves absent
Compressae Trees; branches 2(–3)-winged; leaves absent
Trigonae Trees or shrubs; branches 3(–4)-winged or ribbed; leaves absent
Polygonae Trees, shrubs, or herbs; branches 4–13-ribbed; leaves absent

In 1911 and 1912, N. E. Brown's treatment of *Euphorbia* for the *Flora of Tropical Africa* was published, in which he favored no formal sections within the genus. The arrangement in his account for almost 80 spiny species presented those with single spines first, followed by those with paired spines. The latter were further loosely arranged by habit: dwarf perennial herbs, shrubs, and finally trees. In 1915 he followed a similar pattern for 21 species from the regions covered by *Flora Capensis*.

1911–1912 and 1915. Treatment by N. E. Brown of Spiny Species in *Flora of Tropical Africa* and *Flora Capensis*

Flora of Tropical Africa
  Spines single
    Shrubs or trees; leaves large, persistent
    Herbs or shrubs; leaves very small, deciduous
  Spines paired
    Plants < 1 foot high; flowering branches < 1 inch thick
    Plants > 1 foot high
      Shrubs; flowering branches < 1 inch thick
      Trees; flowering branches > 1 inch thick

Flora Capensis
  Herbs, <1 foot high
  Shrubs, 2–8 feet high
  Trees, 10–30 feet high

Pax presented a more formal classification in 1921 for the 109 African species known at that time, giving subsectional status to his groups. Following his previous (1904) system for section *Diacanthium*, he first listed species in his largest subsection, *Diacanthae*, under countries of origin

(including *E. splendens* from Madagascar), with those of East and South Africa arranged according to branch thickness. He again used the names *Triacanthae* and *Tetracanthae*, partially absorbing *Monacanthae* into *Triacanthae*. *Tetracanthae* contained species arranged according to continuation or separation of the spine-shields and height of the plants. He removed herbs with tuberous roots from his former grouping in *Diacanthae* and adopted Berger's *Scolopendriae* as a subsection to house them. The remaining species in his former *Monacanthae*, *E. venenifica*, and the early species in Brown's system related to it, all with thick cylindrical branches, he placed in a completely unrelated section of the genus—*Treisia* Haw. (1812) (*Euphorbium* Boiss. (1862))—containing plants with spirally arranged tubercles, related to the South African species *E. clava* Jacq.

1921. Formal Classification by Pax of Section *Diacanthium* into Subsections

Diacanthae 2 spines
  Flowering branches > 5 cm thick
    Spine-shields contiguous
    Spine-shields separate
  Flowering branches 2–3 cm thick
Triacanthae 1 (fused) spine, 2 prickles
Tetracanthae 2 spines, 2 prickles
  Spine-shields contiguous
    Herbs to 20 cm high
    Shrubs 1.5 m high or more
    Trees
  Spine-shields separate
    Herbs to 30 cm high
    Shrubs 1 m high or more
    Trees
Scolopendriae Stems short, thick
Section *Treisia* Leaves present, spirally arranged on thick, erect stems

In 1931, Pax & Hoffmann reduced *Diacanthium* to subsectional status under section *Euphorbium* Boiss. (1862), including in the latter all succulent stemmed species of the genus. They adopted Berger's system more fully in order to regroup the now unwieldy numbers of disparate species in Pax's original (1921) concept of *Monacanthae*, *Diacanthae*, and *Intermediae*, using instead all Berger's group names and citing Berger's species as examples. They added to these Pax's own *Triacanthae* and *Tetracanthae*, once more as groups without formal rank.

1931. Classification by Pax and Hoffmann of Section *Euphorbium* subsection *Diacanthium* into Groups

Splendentes Madagascan species
Grandifoliae Spine-shields separate; leaves large
Scolopendriae Herbs with a short thick stem
Compressae Trees; branches 2-winged
Trigonae Trees or shrubs; branches 3(–4)-winged
Polygonae Trees or shrubs
  Branches 3–4-angled
  Branches 4–5(–6)-angled
  Branches 5–8-angled
  Branches 9–13-angled
Triacanthae Shrubs; 1 (fused) spine, 2 prickles
Tetracanthae Shrubs or herbs; 2 spines, 2 prickles

In 1941, White, Dyer & Sloane broke with tradition in devising a more natural sequence for 41 species of spiny *Euphorbia* from South Africa in groups without formal names. These were defined on the basis of habit (dwarf herbs, shrubs, and trees), but position of the capsule and arrangement of the cyathia were also used as important features in deciding relationships.

1941. Treatment by White, Dyer & Sloane of South African Spiny Species

Dwarf herbs, 1 foot high or less
  Capsules exserted
  Capsules sessile
Shrubs, 1–10 feet high
  Branches < 1 inch thick; cyathia horizontally arranged
  Branches > 1 inch thick; cyathia vertically arranged
    Cymes solitary in each flowering-eye
    Cymes 1–4 in each flowering-eye
      Capsules small, exserted
      Capsules large, subsessile
Trees
  Cymes 1–5 in each flowering-eye; cyathia vertically arranged
  Cymes solitary in each flowering-eye; cyathia horizontally arranged

The two latest treatments reverted to the number of branch-angles and spines as criteria for groupings. Jacobsen (1954, 1960) divided all succulent species of *Euphorbia* (but without formal ranking) into *Pedunculicantha* with spines derived from the hardened peduncles of the inflorescence, and *Stipulicantha* with "thorns" derived, he considered, from stipules. This latter group, which concerns us here, he further separated (Jacobsen, 1960) into sections *Euphorbia* (*Diacanthium* of earlier authors and Jacobsen, 1954), *Monacanthium*, and *Triacanthium*. *Euphorbia* was by far the largest of his sections, divided further into two groups (no rank designated), the *Teretes* and *Costatae*, the arrangement within them based on Berger's (1907) treatment. The *Teretes* consisted of the former *Splendentes* and *Grandifoliae*. Within the *Costatae* he enlarged Berger's (1907) and Pax's (1921) concept of the *Scolopendriae* considerably, to include all species with a thick, fleshy, or tuberous root giving rise to tufted branches. The *Trigonae* and *Polygonae* he amalgamated to include all other species—trees, shrubs, and herbs—apart from those in the *Compressae*. Sections *Monacanthium* and *Triacanthium*, with equal status

to *Euphorbia*, he used to accommodate the few remaining single-spined species.

1954 AND 1960. INFORMAL CLASSIFICATION BY JACOBSEN OF SECTIONS AND GROUPS IN *STIPULICANTHA* USING BERGER'S (1907) AND PAX & HOFFMANN'S (1931) ARRANGEMENTS

Euphorbia (Diacanthium) 2 spines
  Teretes
    Group 20 (Splendentes)
    Group 21 (Grandifoliae)
  Costatae
    Group 22 (Scolopendriae)
    Group 23 (Compressae)
    Group 24 (Trigonae and Polygonae)
Monacanthium 1 (fused) spine
Triacanthium 1 (fused) spine, 2 prickles

Rauh (1967) loosely followed this treatment, using sections only: *Monacanthium*, *Triacanthium*, and also *Diacanthium* (instead of *Euphorbia*), which included, once again, the greatest number of species. However, he removed Jacobsen's additions to the *Scolopendriae* to section *Tetracanthium*, adopting for the latter Pax's original (1904) concept of *Tetracanthae* as those species with 4 spines (actually 2 spines and 2 prickles) on each spine-shield.

1967. CLASSIFICATION BY RAUH OF SPINY SPECIES INTO SECTIONS

Diacanthium (Euphorbia) 2 spines; trees, shrubs, and dwarf herbs
Monacanthium 1 (fused) spine; shrubs
Triacanthium 1 (fused) spine, 2 prickles; herbs
Tetracanthium 2 spines, 2 prickles; herbs

All these arrangements have been based primarily on vegetative characters, with features of the inflorescence often ignored as sectional indicators. As an example, N. E. Brown (1911–1912) relied almost entirely on number of branch-angles and detail of the spinescence for dichotomy in his long key. White, Dyer & Sloane's (1941) arrangement was the only one to diverge from this system, using floral as much as vegetative characters to group the South African species. Dyer suggested that in separating the spiny species into related groups, importance should be given to the cyme and cyathial arrangement in each flowering-eye, and the shape of the capsule should also be considered.

Succulence has developed as a device for survival in arid regions. Within the genus *Euphorbia*, adaptation to increasingly arid habitat conditions has involved an increase in succulence of the stem and branches, and a decrease in the size of the plant-body. Representatives of stages in this progression can be found in subgenus *Euphorbia*, ranging in habit from trees, to shrubs, and finally dwarf herbs. The weakest development of succulence—the least advanced state in this adaptation—is found in forest trees with thinly fleshy, winged branches. An increase in succulence of the stem and branches, associated with a decrease in size of the plant-body, is evident in related trees of drier habitats, and in shrubs and herbs of more arid regions, where adaptation to extreme conditions has resulted in the most advanced state: reduction to a small globose body. Other character changes associated with this increased adaptation occur in a reduction in leaf-size, development of the spinescence, the structure of the cyme, a reduction of the perianth-lobes in the female flower, capsule shape and size, and features of the seed.

Comparing features of the least-succulent trees with those of the most-succulent herbs, it is possible to determine which characters have undergone the greatest change during adaptation to an arid environment, and thus which state can be regarded as primitive and which advanced. Apart from a reduction in size linked with habit, from trees to globose-bodied herbs, the large persistent leaves of some trees and shrubs, as would be expected, have given way in most species to very small or minute leaves that are quickly deciduous. The almost rounded, obtusely triangular spine-shields of many trees have become decurrent, which in turn has led to terete branches with spirally arranged tubercles, becoming angled with longitudinal ridges crowned by spine-shields that are sometimes joined to form a continuous horny margin. Stipules, although small, are soft and sometimes almost leaflike in many tree species, whereas in the shrubs, and especially the herbs, they have hardened and been modified into prickles. In most trees and many of the shrubs, several cymes, sometimes branched, are grouped in each flowering-eye, coupled with a vertical arrangement of the lateral cyathia. Most herbs and some shrubs develop one cyme at each flowering-eye, considerably smaller and with lateral cyathia horizontally arranged. Among the trees a 3-lobed perianth is sometimes obvious at the base of the ovary and capsule, which is also relatively large and acutely 3-angled. Usually the perianth is no more than a rim in herbs, shrubs, and many trees, with the capsule reduced in size and obtusely 3-lobed. Finally, although there seems to be no special advantage in such a development, subglobose smooth seeds are characteristic of the trees, but those of most herbs and some shrubs are ovoid and tuberculate.

Using these features and the way in which they have apparently developed within groups of obvi-

TABLE 1. Character states, distribution, and representative species in proposed subsections of sections *Euphorbia* and *Tetracanthae* of subgenus *Euphorbia*.

Subsection	Habit	Leaves	Branches	Spinescence	Cyme arrangement
Section *Euphorbia*					
Euphorbia	Trees	Large, persistent	Terete to winged	Shields triangular, separate	Several in each flowering-eye
Ingentes	Trees and shrubs	Large, persistent or small and deciduous	Winged to angled	Shields triangular, separate, disintegrating	1–many in each flowering-eye
Spirales	Trees and shrubs	Large, persistent	Angled to terete	Shields triangular, separate; spines paired or single	Solitary
Scolopendriae	Small herbs; roots fleshy	Obvious, persistent or small and deciduous	Terete or 2–5-angled	Shields triangular, separate	Solitary
Segmentes	Trees, shrubs, and herbs; roots tuberous	Small, deciduous	Winged, segmented, 2–8-angled	Shields joined or slightly separated	1–many in each flowering-eye
Costatae	Trees and large shrubs	Small, deciduous	Shallowly segmented, 3–7-angled	Shields separated or joined	1–3–many in each flowering-eye
Section *Tetracanthae*					
Sessiles	Shrubs and herbs; roots fleshy or tuberous	Small, deciduous	4-angled, rarely more	Shields separated, rarely joined; spines paired or single	Solitary
Pedicellares	Shrubs and herbs; roots fleshy or fibrous	Small, deciduous	4-angled to 16-ribbed	Shields separated or joined	Solitary

TABLE 1. Continued.

Subsection	Cyathial arrangement	Capsule	Female perianth	Geographical range	Examples
Section *Euphorbia*					
Euphorbia	Vertical	Large, acutely 3-lobed, exserted	Obvious	Thailand west to India, Arabian Peninsula, and northern tropical Africa	*E. lactea, E. neriifolia, E. antiquorum, E. qarad, E. teke*
Ingentes	Vertical or horizontal	Globose, fleshy, just exserted	Obvious	Arabian Peninsula, West Africa, eastern tropical Africa from Sudan south to Natal	*I. ammak, I. kamerunica, I. abyssinica, I. ampliphylla, I. ingens*
Spirales	Horizontal	Large, acutely 3-lobed, exserted	Reduced to a rim	West and central tropical Africa	*S. desmondii, S. sudanica, S. poissonii, S. venenifica*
Scolopendriae	Horizontal	Acutely 3-lobed, exserted on a recurved pedicel	Reduced to a rim	Angola to Mozambique and south to the Cape	*S. imitata, S. decidua, S. knuthii, S. stellata*
Segmentes	Vertical	Large, acutely 3-lobed, subsessile	Obvious or reduced to a rim	Arabia and Somalia south to Mozambique and west to Angola, Namibia, and the Cape	*S. cactus, S. ballyi, S. nyikae, S. breviarticulata, S. cooperi, S. grandicornis, S. enormis*
Costatae	Vertical or seldom horizontal	Large to small, angled to lobed, exserted	Reduced to a rim	Somalia south to Mozambique, Angola, Namibia, and the Cape	*C. robecchii, C. wakefieldii, C. confinalis, C. parviceps, C. grandidens, C. griseola*
Section *Tetracanthae*					
Sessiles	Horizontal	Small, obtusely lobed, subsessile	Reduced to a rim	Arabia and Somalia south to Mozambique, Angola, Namibia, and the Cape	*S. triaculeata, S. polyacantha, S. uhligiana, S. angustiflora, S. malevola, S. schinzii*
Pedicellares	Horizontal	Small, obtusely lobed, exserted on a recurved pedicel	Reduced to a rim	Arabia, Socotra, northeast and eastern tropical Africa	*P. fruticosa, P. spiralis, P. phillipsiae, P. turbiniformis, P. heterochroma*

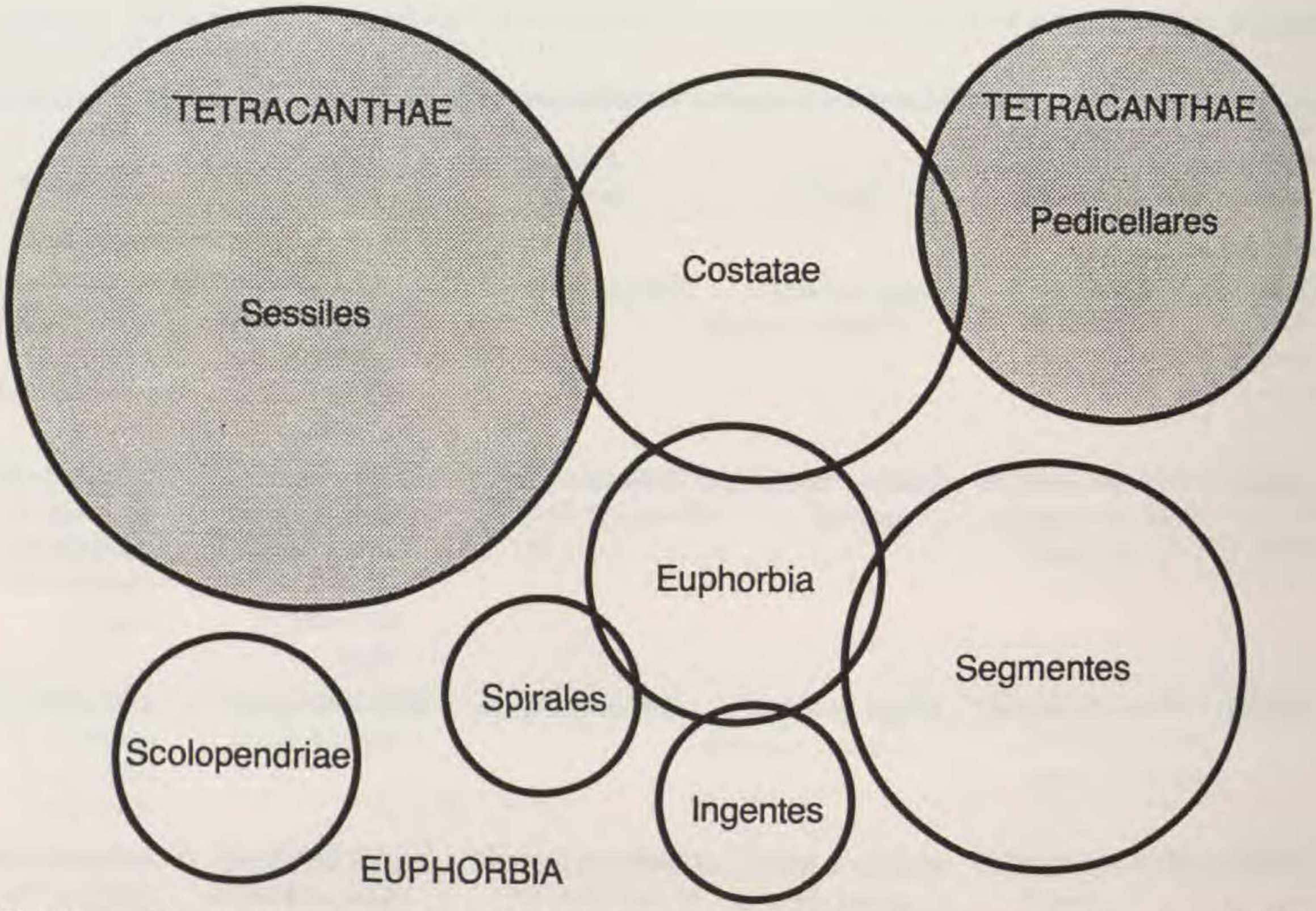

FIGURE 1. Diagramatic representation of relationships between groups (subsections) within subgenus *Euphorbia*, with two sections: *Euphorbia* and *Tetracanthae*. Circle-size is proportional to the number of species in each subsection.

ously closely related species, an outline scheme for the classification of the 250 plus species in subgenus *Euphorbia* is presented here, with two sections and several possible groups or subsections. Inevitably, there is some sharing of character states between groupings, and this has been used to indicate trends in development. The most obscure relationships occur between the smaller groups containing species exhibiting an early, more primitive stage in development, whereas those with features at the most advanced stage are the most easily defined. These are also represented by a much larger number of species, among which obvious subgroups or series have emerged, with some apparently still developing. However, characteristics of the seed are consistent within groups, and this feature is used to separate the subgenus initially into two sections: section *Euphorbia*, containing species with more primitive character states, and all with smooth, globose or subglobose seeds; and section *Tetracanthae*, containing species with more advanced characteristics, all with tuberculate, more-or-less ovoid seeds (see Fig. 1 and Table 1).

Among the few representative species (about 12–15) of the subgenus in India, Malaysia, and the Far East, all possess features at a stage regarded here as primitive, with only slight modifications in some species toward an adaptation for survival in a drier environment. As an example, *Euphorbia neriifolia* L. is a tree, with terete branches, rounded spine-shields spirally arranged, large leaves (to 30 cm long), triangular flexible stipules, several long-pedunculate branching cymes from each flowering-eye, a lobed perianth below the ovary, an exserted deeply lobed capsule, and smooth globose seeds. *Euphorbia antiquorum* L. is modified only slightly in its obscurely 3-angled branches, smaller, less persistent leaves, and fewer-branched cymes. Other species show a greater tendency toward both angled branches and reduction in leaf size. To the west, in the Arabian Peninsula, *E. qarad* Deflers shows a reduction in size to a large shrub and to very small deciduous leaves. In the African continent, primitive states are most evident in a group of probably four closely related species from the forest region of western Uganda westward across northern Zaire to Cameroon. These include *E. teke* Pax, modified only in its obscurely 4-angled branches.

This group of species, with characters at the most primitive stage of development, corresponds most nearly with Berger's (1907) group *Grandifoliae* and Jacobsen's (1960) *Teretes*, excluding the *Splendentes*. Since it contains the type species of the genus it must, under present rules, be referred to as *Euphorbia* at whatever rank.

Several groups (or possible subsections) appear to have developed from this basic group ("subsec-

tion *Euphorbia*"), with different features undergoing change. One that I propose calling the "*Ingentes*" accommodates about 10 species with a wide distribution covering most of the African continent and beyond to the Arabian Peninsula. Modifications shared by all its species are angled or sometimes winged branches, with more closely set spine-shields disintegrating at maturity to become corky and powdery, simple cymes and only slightly exserted, usually fleshy subglobose capsules, which nevertheless harden and become acutely 3-lobed at dehiscence. *Euphorbia ampliphylla* Pax (*E. obovalifolia* auct. non A. Rich.), the species most closely related to those of "subsection *Euphorbia*" has 3–4 deeply winged, thinly fleshy branches, and large leaves (to 15 cm long) persistent on young growth. It is the largest of all *Euphorbia* species, reaching 30 m in height, surviving only in mist forests above 1800 m, from Eritrea southwards to northern Zambia and Malawi. At lower altitudes most species show an increase in succulence of the branches and decrease in leaf size. *Euphorbia ingens* Boiss., from southern Africa, has more fleshy, angled rather than winged branches, and leaves smaller (to 7 cm long) on seedlings and young growth, but tiny and deciduous on mature growth. *Euphorbia abyssinica* J. F. Gmel., from drier regions of northeast Africa, is very similar, but has stouter, 5–8-angled branches. The closely related *E. ammak* Schweinf. occurs in the Arabian Peninsula, and *E. kamerunica* Pax, a 4-winged species, in West Africa. *Euphorbia canariensis* L., from the Canary Islands, appears to share most features of this group but also shows the most extreme modifications. It is a large shrub instead of a tree, with single simple cymes, horizontally instead of vertically arranged cyathia, and capsules that are only slightly fleshy. Members of this group have previously been placed with other unrelated species depending on the number of branch angles.

A group here called the "*Spirales*" accommodates about nine very distinct, closely related species with a limited distribution in West and Central Africa. Modifications found in such species as *Euphorbia desmondii* Keay & Milne-Redh. and *E. sudanica* Chev. are evident as a reduction in size to shrubby trees, angled branches, solitary cymes with cyathia arranged horizontally, and the perianth of the female flower reduced to a rim. Specialization has led to a subgroup of smaller shrubs that have spine-shields so densely placed in numerous spiral series that thick cylindrical branches have resulted. Furthermore, the paired spines appear fused together early in the seedling stage, after which only single spines are produced. These later deteriorate so that the mature plants sometimes appear to be entirely without spines. *Euphorbia venenifica* Kotschy and *E. poissonii* Pax are typical of this subgroup, one that Pax and other authors had such difficulty in placing.

Reduction to tuberous-rooted herbs has taken place in one group, which has been apparent as distinct since Boissier's (1862) classification, and which even now is difficult to relate to other groups. This was given the name *Scolopendriae* by Berger and formalized as a subsection by Pax (1921). Its species, all from southern tropical Africa, are small herbs or geophytes, characterized by a large tuberous root, extremely short stem branching at or below ground level, small rounded spine-shields, and acutely lobed capsules exserted on a recurved pedicel.

Two series appear to have developed within the group. In one, a progression can be shown from thin branches with very small spine-shields and spines, as in *Euphorbia knuthii* Pax, to leafless angled or winged branches with strong spines, as in *E. stellata* Willd.

The second series, in a group of closely related species, shows a progression from such species as *Euphorbia imitata* N. E. Br., with persistent leaves, to *E. decidua* P. R. O. Bally & L. C. Leach, with a development of the tuberous root to a spherical body from which deciduous branches develop separately from the cymose inflorescences, bearing tiny deciduous leaves and small rounded spine-shields.

The most probable relatives of the group seem to be species in "*Spirales,*" through a common ancestor and an early reduction of the shrubby form. Similarities between the two groups lie in the rounded spine-shields, persistent leaves, cyme and cyathial structure and position, and especially the sharply angled exserted capsules with smooth globose seeds.

Another easily defined group within section *Euphorbia* is one I propose calling the "*Segmentes,*" incorporating Pax's *Intermediae.* Some primitive features are retained, namely several cymes at each flowering-eye together with vertically arranged cyathia, often an obvious lobed perianth, large acutely 3-lobed capsules, and smooth globose seeds. There are some tree species, but most are shrubs; branches are distinctly winged and constricted at intervals into rounded or oblong segments; the spine-shields have become so decurrent that in almost all species they have joined to form a horny margin along the branch-angles, often very stout and occasionally giving rise to further spines flanking the flowering-eye (Pax's *Intermediae*); leaves are tiny and deciduous, with stipules hardened into very short or usually rudimentary prick-

les. One of the least advanced species is *Euphorbia nyikae* Pax from East Africa, bearing some similarity to *E. lactea* Haw. from Sri Lanka in "subsection *Euphorbia*," but with decurrent spine-shields.

The 40 or more species within the "*Segmentes*" show a reasonably successful adaptation to an increasingly arid environment. The tendency is toward a reduction in size to shrubs, and eventually fleshy herbs, together with an increase in the size of the rootstock to large and tuberous. At the same time, the capsule becomes subsessile among most of the shrubs, and totally sessile in the herbs. Several series of species show this progression. In East Africa, for example, there are a tree species *Euphorbia bussei* Pax, a shrub *E. breviarticulata* Pax, and a tuberous-rooted herb *E. buruana* Pax. Further south a similar progression is shown by the tree *E. cooperi* A. Berger, the shrub *E. grandicornis* N. E. Br., and the herb *E. enormis* N. E. Br.; while in the more extreme habitat conditions of Angola and Namibia shrubs such as *E. coerulescens* Haw. and tuberous-rooted herbs related to *E. opuntioides* Hiern may be found. The complex is distributed as far north as the Arabian Peninsula, with the shrub *E. cactus* Schweinf., and in northern Somalia the shrub *E. ballyi* S. Carter together with an unnamed dwarf tuberous-rooted species.

A most diverse group of species, with variable characteristics and also a wide distribution, has close relationships with "subsection *Euphorbia*," but differs consistently in a number of distinct modifications. Among primitive features, most species are trees and most have several cymes at each flowering-eye, with vertically arranged cyathia. However, some species have a tendency to develop a shrubby habit, and cymes become solitary, with the cyathia arranged horizontally. Branches are always angled (3–7), giving the group its name of "*Costatae*" (Jacobsen's (1960) name without formal rank), and occasionally winged, with spine-shields decurrent and either separate or forming a continuous horny margin. Leaves are tiny and quickly deciduous, but stipules are sometimes obvious and flexible—a primitive feature—or more usually are present as rudimentary prickles or are only vestigial. The perianth is reduced to a rim. Pedicel length of the capsule is variable, as is capsule size, with the larger capsules usually acutely angled on stout, often curved pedicels, and the smaller ones more obtusely lobed on slender recurved pedicels.

A number of tree species from Angola related to *Euphorbia edouardii* L. C. Leach and *E. parviceps* L. C. Leach have retained most of the more primitive features, which they share with such species as *E. robecchii* Pax from East Africa, and *E. evansii* Pax and *E. confinalis* R. A. Dyer from further south. *Euphorbia robecchii* in turn seems to bear some relationship to *E. qarad* in "subsection *Euphorbia*," through an unnamed intermediate shrubby tree that occurs in Djibouti.

In East Africa a series of several tree species with limited distributions has developed, including the narrowly 3-winged *Euphorbia wakefieldii* N. E. Br. with small triangular spine-shields and *E. quinquecostata* Volkens with 5-angled branches and decurrent spine-shields that become joined as growth matures. Both species have small, obtusely lobed capsules that are well exserted. This series culminates in *E. classenii* P. R. O. Bally & S. Carter, a 1-m-high shrub with 6–8-angled branches, decurrent spine-shields, solitary cymes with horizontally arranged cyathia, exserted capsules, and smooth, more or less ovoid seeds.

A comparable series has arisen in southern Africa, including the tree species *Euphorbia grandidens* Haw., with 3-angled branches, small triangular spine-shields, and slightly exserted capsules, and *E. zoutpansbergensis* R. A. Dyer, with 6-angled branches, decurrent spine-shields becoming joined, and obtusely lobed, exserted capsules. Shrubby species such as *E. avasmontana* Dinter, with a stout horny margin to usually 5-angled branches, have developed especially in the semi-desert regions of southwest Africa.

Most of these species have a tendency to produce more than one cyme at each flowering-eye, with vertically arranged cyathia. However, *Euphorbia griseola* Pax, from south tropical Africa, is one species that has developed as a small tree with a short trunk (subsp. *zambiensis* L. C. Leach) and also as a low-growing spreading shrub (subsp. *griseola*), but always with decurrent spine-shields sometimes joined, solitary cymes with horizontally arranged cyathia, and small, well-exserted, deeply lobed capsules containing smooth globose seeds. A further development has produced a series of a few species related to *E. perangusta* R. A. Dyer, with the fleshy root developed into a large tuber, and decurrent spine-shields on short winged branches that have become almost segmented. These bear a superficial resemblance to the reduced herbs of the "*Segmentes*," the overriding difference being that capsules are small and well exserted instead of large and sessile.

Several of the 40 or so species in this widely distributed group "*Costatae*" can be considered as linking species with those in the two groups that have been the most successful in terms of species

numbers and adaptation to arid conditions. These show the most advanced and none of the primitive character states postulated for "subsection *Euphorbia*." Also, one outstanding feature that all the species possess is an ovoid tuberculate rather than globose and smooth seed. On this basis I have separated them into section *Tetracanthae*, which Pax (1921) formalized and which included very few species regarded here as belonging instead to section *Euphorbia*. Pax's (1921) definition of the section allowed for the inclusion of all species bearing four spines on the spine-shields. However, this is exceedingly misleading. All species within the larger category of subgenus *Euphorbia* bear two spines, outgrowths from the horny pad surrounding the base of the leaf, together with a pair of stipules that are evident in every species. These stipules can be triangular, flexible, and almost leaflike in some tree species with more primitive characteristics; or they can be modified into obvious prickles or occasionally short spines in species at a more advanced stage of development. They can equally be rudimentary or visible only with a powerful hand lens among species of most groups (or subsections) in section *Euphorbia* and in both groups of section *Tetracanthae*. However, within this latter section, modification into a pair of obvious prickles is a hallmark, although by no means universal, of the larger group—called here "subsection *Sessiles*"—the definitive feature being a small, obtusely lobed sessile or usually subsessile capsule, at the most only just exserted from the involucre. Species in the smaller, totally distinct group—"subsection *Pedicellares*"—also possess a small obtusely lobed capsule, but this is always well exserted on a slender recurved pedicel. Stipules are evident as short prickles, or more often are rudimentary or vestigial. In both subsections, herbs with an often large fleshy root predominate, with relatively few shrubs, which are rarely more than 1 m high. Other advanced features lie in tiny deciduous leaves, decurrent spine-shields, solitary cymes with horizontally arranged cyathia, and the perianth reduced to a rim.

The "*Sessiles*" includes more than 80 species, distributed mostly in eastern and southern tropical Africa, but extending also to southwest Africa, and northeastward to the Red Sea Hills of Sudan and the Arabian Peninsula. With few exceptions branches are 4-angled, with decurrent spine-shields that are seldom joined. Some species in the "*Costatae*" can be regarded as providing a link with other, usually shrubby and possibly related species in the "*Sessiles*," but despite similarities in spinescence and inflorescence characters, the difference between ovoid tuberculate seeds and globose smooth seeds always provides a positive means for sectional identification. *Euphorbia dumeticola* P. R. O. Bally & S. Carter in the "*Costatae*" is a small tree from central Tanzania with solitary cymes, horizontal cyathia, and only shortly exserted capsules, which is perhaps related to the shrub *E. proballyana* L. C. Leach in the "*Sessiles*," endemic in the same area. Similarly, several species from southern Africa in the "*Costatae*," e.g., the shrub *E. waterbergensis* R. A. Dyer, which possesses shortly exserted, obtusely lobed capsules, suggest a possible link with shrubs such as *E. lydenbergensis* R. A. Dyer in the "*Sessiles*."

As would be expected in a large group at such an advanced stage of adaptation, a number of distinct subgroups, or series, of closely related species have evolved. For example, in southern Africa, *Euphorbia schinzii* Pax is one of a number of very similar species with spreading tufts of short erect branches and, itself, is identified in several forms, differing in stem thickness and spine color. The strange *E. corniculata* R. A. Dyer, from Mozambique, with enlarged spine-shields and apparently obsolescent prickles, appears to be related. Further north, the more shrubby *E. malevola* L. C. Leach from Zimbabwe has obvious affinities with *E. ambroseae* L. C. Leach from Mozambique and in turn *E. isacantha* Pax from southern Tanzania. One small subgroup of distinctive species with almost peltate involucral glands, related to *E. angustiflora* Pax, is confined in distribution to central and southwest Tanzania. Other subgroups have evolved in East Africa, such as *E. uhligiana* Pax and its relatives, all with a distinctive T-shaped spine-shield, and the development among species from more arid areas of a vertical series of cymes that mature in succession in each flowering-eye. Several forms have emerged with extreme modifications of the spinescence: the rhizomatous species *E. taruensis* S. Carter from Kenya has extremely slender spine-shields bearing obvious prickles, but spines that are rarely more than rudimentary; and the subscandent *E. cryptospinosa* P. R. O. Bally has usually 7-angled stems, with spine-shields joined into wide continuous ribs and minute spines on young growth only that cannot be seen except with the aid of a hand lens.

Besides *Euphorbia cryptospinosa* from Kenya and relatives in southern Somalia, species with more than four angles have also evolved in southwestern Africa, e.g., *E. kaokoensis* L. C. Leach. In the northeast, as far as the Red Sea Hills in Sudan, *E. polyacantha* Boiss. has developed into a 6–7-angled shrub with a stout spinescence. A related unnamed species with more slender 4–5-angled

branches occurs throughout the hilly regions from Djibouti eastward across northern Somalia.

A feature that has developed principally among plants of drier regions in the northeast is the fusion of the paired spines in the seedling stage, when this is no more than 2–3 cm high, to produce what appears to be a single spine. The presence or absence of prickles led former workers to mistakenly separate these species into groups with one or three "spines" (e.g., Pax's (1904) *Monacanthae* and *Triacanthae*), including the shrubs related to *E. venenifica*. One subgroup, *Euphorbia graciliramea* Pax and its relatives, has developed in the Rift Valley of northern Tanzania and southern Kenya as herbs with a large fleshy root producing tufts of short branches and small spine-shields with rudimentary prickles. Another group from northern Kenya and Ethiopia, related to *E. monacantha* Pax, has developed a short thick stem with numerous branches radiating from a central growing point and varying in length between species. Other species without this distinctive "medusoid" habit can be related to *E. triaculeata* Forssk. from the Arabian Peninsula. Several unnamed species in this subgroup occur in Somalia and eastern Ethiopia. Intermediate forms, with spines only partly fused, are found in *E. schizacantha* Pax, with a short, thick, many-angled stem and thin, trailing, 4-angled branches; and *E. glochidiata* Pax, with a 2-m-high stem and undifferentiated branches. Both species and their relatives occur in the dry deciduous bushland of northeast Kenya, southeast Ethiopia, and southern Somalia.

Within subgenus *Euphorbia*, the most successful adaptation to a hostile environment is shown by members of "subsection *Pedicellares*." The group has diversified in east and especially northeast Africa, with representatives also in the Arabian Peninsula and Sococtra, and a disjunct distribution in Morocco and the Canary Islands.

At the southern limit of distribution of this group, in northeast Tanzania, *Euphorbia heterochroma* Pax is a shrub to 2 m high with 4-angled branches, evidently related to *E. classenii* in the "*Costatae*," which differs in its 6–8-angled branches and distinctly separated spine-shields, as well as its smooth globose seeds. In drier inland areas in Kenya, Uganda, and southern Ethiopia, *E. heterochroma* gives way, in an obvious progression, to shorter more sturdy shrubs, with up to 8 angles, and spine-shields joined in a wide horny margin, culminating in the various forms of *E. tescorum* S. Carter.

In Somalia and the Ogaden region of eastern Ethiopia, adaptation to the very specialized semi-desert conditions created by a limestone soil and outcrops of pure gypsum has led to the development of many narrowly endemic species. Stems and branches have become many-angled—up to 18—and reduced in size, finally to a globose body, evident in several species. *Euphorbia columnaris* P. R. O. Bally presents one extreme, as an unbranched stem with up to 16 angles and a cluster of up to 30 cymes, maturing successively, at each flowering-eye. *Euphorbia turbiniformis* Chiov. presents another, as a small spherical body that is almost buried in the soil and has lost all its spines. *Euphorbia gymnocalycioides* M. G. Gilbert & S. Carter is an intermediate form, with up to 18 ridges of tubercles crowned by tiny, weakly horny spine-shields occasionally bearing vestigial spines. *Euphorbia piscidermis* M. G. Gilbert belongs here also, having developed a globose body and an extreme modification of the spine-shield into a fringed "scale," with a pair of minute spines evident only on tiny seedlings.

There are numerous species from Somalia (many still unnamed) in several series, leading to similar extremes, usually in the form of dwarf "cushion"-forming plants with 5 to many angles on short, densely packed branches. Some have small, distinctly separated spine-shields, like *Euphorbia ellenbeckii* Pax, while others have narrow horny margins along the angles, like *E. phillipsiae* N. E. Br.

In common with other examples in Africa of a northeast-northwest relationship, a disjunct group of species with obvious similarities occurs in the Canary Islands and Morocco. Several shrubby species related to *Euphorbia echinus* Hook.f. & Coss., from the Moroccan coast, possess many-angled branches and spine-shields joined in a narrow margin along the angles, as well as small capsules exserted on recurved pedicels.

Other species of the "*Pedicellares*" extend into the Arabian Peninsula in at least three forms of *Euphorbia fruticosa* Forssk. and occur in Socotra as *E. spiralis* Balf.f. The large shrub *E. abdelkuri* Balf.f. from Socotra, with 6–8-angled, spineless branches, also belongs here, the spines and spine-shields having been lost during the process of evolution (but which are nevertheless present at the seedling stage), possibly due to the absence of browsing animals on a small island.

Subgenus *Euphorbia* is arguably the most easily and satisfactorily defined of all the major groups within the genus, at whatever rank, and as such could be separated as a genus in its own right (which begs the question: what to do with all the other groups not as readily separated as *Chamaesyce*?). It shows as great, if not a greater, diversity